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Research Article

Conservation of the Lion: Preventing an Africa without the African Lion

—Courtney Kamyk

I never thought I would find myself sitting in a Land Rover on a peaceful afternoon watching twelve lions nap off their meal from the previous evening under a shady tree. As I looked out into the tall grass and surrounding trees, it all seemed surreal. I smiled with the warm African sun on my face as Zulu, the lion pride male, lazily rolled over and yawned.

As a young girl, I was drawn to big cats and Africa. I watched any and every show about the African savannah, and *The Lion King* remains my favorite movie of all time. I had no idea my childhood dream of working with big cats in Africa would one day come true. The summer after my junior year at the University of New Hampshire (UNH) I was awarded an International Research Opportunities Program (IROP) grant to study African lion (*Panthera leo*) behavior in Livingstone, Zambia. I was excited to apply what I had learned in the classroom and gain preparation for veterinary school by exposing myself to the world of both research and wildlife medicine.

Before this project, I was oblivious to the serious dangers that threaten wild lion populations in Africa. I have since learned the harsh reality that the African lion is facing. I partnered with the African Lion and Environmental Research Trust (ALERT), a non-governmental organization that works in Zambia and Zimbabwe to conserve the African lion. The organization uses a multifaceted approach to decrease human-lion conflicts and to increase lion populations. By focusing largely on community and conservation education, ALERT is able to reform local opinions of the lion and act to preserve and increase current lion populations.

One of the programs in place at ALERT is a type of ex-situ conservation, in which individuals are raised in captivity and allowed to raise offspring born into a wild setting and then offspring are released into the wild later in life (Biggins, Vargas, Godbey, & Anderson, 1999). Successful ex-situ conservation has been implemented in many species, such as the guar, the California condor, and the whooping crane. A better understanding of the intricacies of lion behavior and personalities could aid in selecting



The author with a lion from one of the Zimbabwean ALERT sites.

individuals more likely to succeed in the wild after reintroduction. With the help of my UNH mentor, Dr. Drew Conroy, and my foreign mentors at ALERT, Dr. Emma Dunston and Dr. Jackie Abell, my study aimed to address how the personality trait of boldness in African lions correlates with natural behaviors such as resting, aggression, play, and other social behaviors in the Dambwa lion pride located in Livingstone, Zambia.

Importance of Animal Personalities

Boldness is a personality trait important in individual and species survival (Bremner-Harrison, Prodohl, & Elwood, 2004). Animal personalities are defined as correlations among behavior across contexts and in different situations (Sih, Bell, Johnson, & Ziemba, 2004a; Sih, Bell, & Johnson, 2004b). Animal personality influences social structure and group dynamics (Dunston et al., 2017). Previous research in different species suggests that boldness may be related to postrelease survival (Bremner-Harrison et al., 2004; Sinn, Cawthen, Jones, S., Pukk, C., & Jones, M.E., 2014; Dunston et al., 2017; Greenberg & Holekamp, 2017). A meta-analysis of boldness conducted by Smith and Blumstein (2008) concluded that boldness consistently shows a negative correlation with survivorship across species. However, bold individuals had higher reproductive success across species, suggesting a trade-off between survivorship and reproductive success.

One factor known to result in reintroduction failure is that captive-raised individuals are behaviorally inept for survival within challenging situations of the wild (Watters & Meehan, 2007). The captive environments do not always offer the same challenges as wild ones, so captive individuals may not develop necessary survival skills. By studying animal personalities, key species-specific behaviors necessary for survival can be identified, allowing for the reintroduction of animals most suited for survival (Watters & Meehan, 2007). Within ex-situ reintroduction programs, assessing boldness has been found effective in predicting postrelease survival (Bremner-Harrison et al., 2004; Sinn et al., 2014). This provided the foundation for my research project.

A Look into Lion Populations

The importance of implementing conservation programs, such as ex-situ reintroduction, is highlighted by the recent decline in lion populations. Once very widespread, lions ranged from southern Africa to Central America during the Late Pleistocene era, about 12,000 years ago (Barnett et al., 2009). Today's lion populations are confined to parts of Asia and Africa.

In 1996, the lion was listed by the International Union for Conservation of Nature's (IUCN) Red List as vulnerable. In 1975, lion populations were at an estimated 200,000 (Myers, 1975). By the 1990s, it was believed that fewer than 100,000 remained (Nowell & Jackson, 1996). The most current estimates of lion populations range from 33,000 to 35,000 (Bauer, Packer, Funston, Henschel, & Nowell, 2016; Riggio et al., 2013). However, the overall IUCN classification of vulnerable masks an unfortunate dichotomy. From the early 1990s to 2014, lion subpopulations increased by 12 percent in four southern African countries (Botswana, Namibia, South Africa, and Zimbabwe) and in India. However, populations across the rest of the species' African range declined by 60 percent (Bauer et al., 2016). Based on this 60 percent decline in some subpopulations, the lion would meet the IUCN

criterion for endangered, but the overall population trend does not meet these IUCN classification requirements (Bauer et al., 2016). The African lion in northern and western Africa is listed as endangered, but in southern and eastern Africa the species is listed as vulnerable. The IUCN estimated the lion population of Zambia, where I conducted research, in 2009 to be 1,750 individuals; today the estimate is a mere 230 (Bauer et al., 2016).

The most critical cause of decline is habitat loss and fragmentation due to the increase in human populations and the extensive conversion of land to human use. Worldwide, current lion populations occupy about 25 percent of available habitat suitable for lions (Riggio et al., 2013). However, habitats across this area are highly fragmented, leading to the additional issues of decreased genetic diversity and an increase in inbreeding. Another cause of decline is prey depletion, which is partially linked to habitat loss, but more importantly to poaching and the bush meat trade (Becker et al. 2013).

A third cause of decline is the killing of lions in defense of human life and livestock (Hemson et al., 2009). Many Africans have a negative perception of lions and believe that they are the cause of many livestock and human deaths associated with predators (Hemson et al., 2009). As a result, people may actively trap and/or kill lions, even if the lions themselves are not responsible for the livestock or human deaths (Hemson et al., 2009).

Other causes of decline include trophy hunting and an introduction of new diseases, such as tuberculosis (Whitman et al., 2004; Michel et al., 2006).

Although the exact degree of decline is debatable, it is clear that the African lion population could become severely threatened in the near future if no action is taken. Ex-situ conservation programs like those being conducted at both the Zambian and Zimbabwean locations of ALERT are critical to sustaining lion populations.

On the Ground

During my stay at ALERT in Zambia, I conducted my own research project as a facilitated research intern. The organization is continually collecting research of its own with the help of volunteers and interns from around the world in order to further understand the African lion. Emma Dunston, my mentor and the head lion researcher at ALERT at the time, oversaw my project and helped me to collect data during my short stay.

In Africa, I stayed at a site called Serenity, which is composed of ten chalets that each house one to three ALERT volunteers and/or interns. I enjoyed having roommates; it exposed me to more cultures and people from around the world. Meals of surprisingly American food (sandwiches, spaghetti, stir fry, chicken fingers) were provided by the adjacent restaurant, The Old Farmhouse. Occasionally, everyone staying at Serenity would go out to dinner in Livingstone, one of Zambia's best-known tourist towns, for a more authentic meal, such as impala stew. Some interns and volunteers were even brave enough to try the crocodile pizza.

The lions I studied were located approximately twenty minutes away from Serenity by Land Rover, over twisty, bumpy, dirt roads through the Mosi-oa-Tunya National Park. The Dambwa pride is

located in the Dambwa Forest, eight kilometers from the city of Livingstone, Zambia. The site is a mixture of woodland and shrub land, with some small grassland areas.

The pride comprises six adults and six offspring (Figure 1). The adults were born in captivity in 2008 and were released into the fenced, 707-acre Dambwa site in 2011, where they live and reproduce as a pride. Their first litter of offspring was born to mother Rusha and father Zulu on June 30, 2013, and consisted of one male and two females. The second litter was born to mother Leya and father Zulu on January 30, 2014, and consisted of one female and two males. These six offspring, who are considered sub-adults, will be released into the wild when they are physically and reproductively mature at around five to six years of age.



Figure 1: Twelve lions make up the Dambwa pride at ALERT in Zambia. The dominant male is Zulu, and the dominant female is Rusha. Other adult females include Kwandi, Kela, Loma, and Leya. Rusha is the mother to 4-year-old offspring RS1 (female), RS2 (male), and RS3 (female). Leya is the mother of 3.5-year-old offspring LE1 (male), LE2 (female), and LE3 (male).

Research Methods

Each day at ALERT, I climbed into our research vehicle, a Land Rover called Doris, along with my mentor, a guide, and other interns and volunteers. We set out early in the morning to find the pride in their release site. From the

research vehicle, we used a variety of visual observation techniques to collect various types of behavioral data on each individual lion of the pride.

I recorded all witnessed social interactions and categorized each as greet, groom, play, or aggression in a field notebook. Greet interactions were determined as one lion approaching another and rubbing its head or length of body along the other. Groom interactions were defined as allogrooming, where one individual licked another. Play behavior was determined as affiliative behavior between two individuals with no intent to threaten or harm. In contrast, aggression was viewed as behavior intended to threaten, deter, or harm.

I organized social interactions in my assigned categories each week and tallied all social interactions. At the end of my data collection, I analyzed each group of interactions using the social network analysis program UCINET (Borgatti, Everett, & Freeman, 2002). I then used NETDRAW (Borgatti et al., 2002) to generate sociograms for each matrix, providing a visual representation of all social, greet, groom, play, and aggression interactions observed within the pride (Figure 2).

To determine each lion's boldness, I observed individual reactions to a series of six playbacks. A playback is a recording of another animal or lion's vocalizations that is played through a hidden speaker. I observed how the lions of the pride reacted to the unfamiliar sound each time it was played.

I used two types of playbacks: appetitive and territorial. Appetitive playbacks were used to elicit a food response from the pride and to test boldness in food-specific instances. The three appetitive playbacks used were "hyena on a kill," "zebra alarm calls," and "African wild dog on a kill." The playbacks used to test boldness in territorial instances were the territorial calls of "a male leopard," "unfamiliar lions, mixed sexes," and "four unfamiliar male lions."

In order to ensure that the lions would not become accustomed to the playbacks, we played them at a minimum of five days apart. Just before the playback began, I observed individual behavior to provide a baseline for each lion. The recording played from outside of the release site with a BOSE SLIII speaker system, a minimum of 200 meters from and out of view of the lions (Dunston et al., 2017). I made my observations from a research vehicle the lions were familiar with to ensure the lions reacted to the playbacks themselves instead of an unfamiliar vehicle. Once the playback began, I noted the reactions of all visible lions until all lion behaviors indicated a return to uninterested behavior, such as sleeping or grooming. All behavior recordings were ceased after thirty minutes. At the end of each test, I used a scoring system to determine boldness scores for individual lions (Appendix A).

At the end of each session, I calculated a total score for each playback for each individual lion present. A higher score indicated that a lion was bolder in their response. In order to analyze results, I used Microsoft Excel to calculate the average appetitive score, average territorial score, and average overall boldness score for each individual lion.

When I was not collecting playback data, I recorded behaviors of all present individuals in sixty-minute sessions, sampling every two minutes. From this data, I composed an average daily activity budget using an ethogram, a detailed table of all daily behaviors, of the lions. I calculated the average percentage of time each lion performed each recorded behavior and the pride average per behavior. I also calculated the pride average percentage of daily activity, as represented in Figure 3.

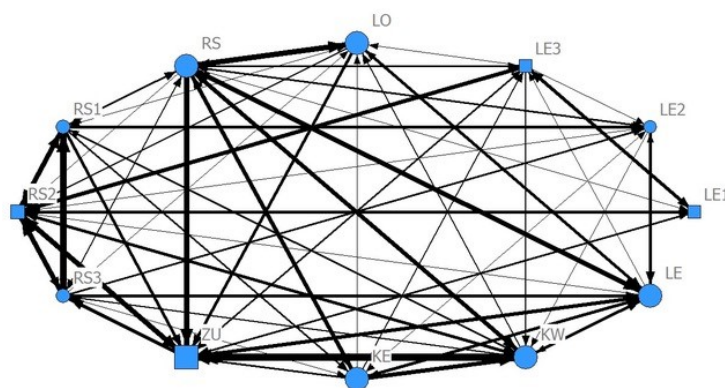


Figure 2: Sociogram of all social interactions between the twelve individuals of the Dambwa pride. Nodes represent individual lions, with node shape indicating the sex (square = male, circle = female). The size of the node correlates with the age of the lion, with a smaller node indicating a younger lion, and a larger node indicating an older lion. Lines between nodes represent interactions between lions, with arrows showing the flow of the interaction from initiator to receiver. Line thickness is directly proportionate to the number of interactions observed between lions, with a thicker line indicating more interactions between individuals.

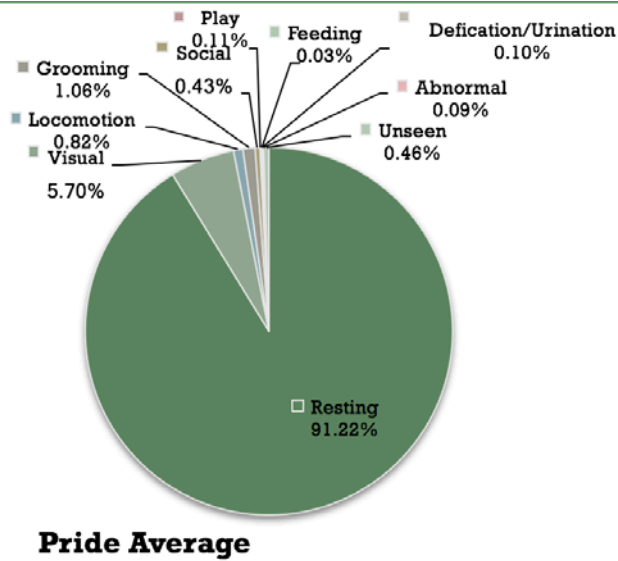


Figure 3: Average percentage of daily activity, shown as a pride average.

To assess the significance of correlations between sociality, average percentage daily activity, and boldness, I used the statistical program Genstat, 18th edition (VSN International 2014).

Interpreting the Data

I observed that individuals with higher appetitive playback scores, meaning those who reacted more boldly to playbacks related to food, were predominantly female (Figure 4). These lions initiated more social interactions and were overall more social than those with lower appetitive scores. They were also more central to the groom network. The statistical significance of these correlations may be seen in Appendix B.

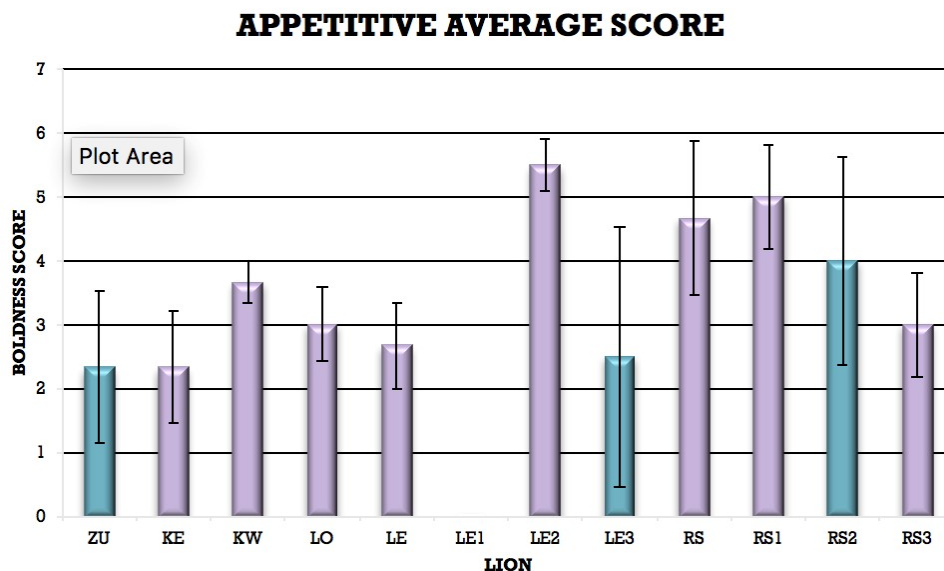


Figure 4: Average appetitive boldness scores for the individual lions of the Dambwa pride. Male lions (ZU, LE1, LE3, RS2) are differentiated with blue bars. Females (KE, KW, LO, LE, LE2, RS, RS1, RS3) are represented by purple bars.

As with appetitive playbacks, I observed that lionesses had higher territorial playback scores than males (Figure 5). This was especially interesting because male lions in wild prides are typically seen defending territory from competing prides more than females, so one would expect males to have higher territorial scores (Packer & Pusey, 1997). My findings could be due to the fact that the pride male, Zulu, was the same age as the adult females of the pride, and raised in captivity alongside

TERRITORIAL AVERAGE SCORE

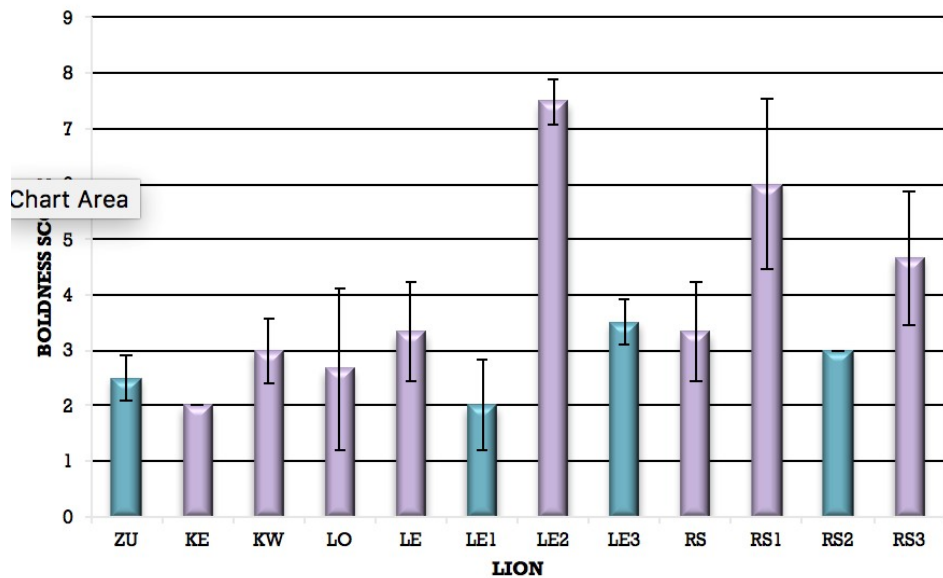


Figure 5: Average territorial boldness scores for the individual lions of the Dambwa pride. Male lions (ZU, LE1, LE3, RS2) are differentiated with blue bars. Females (KE, KW, LO, LE, LE2, RS, RS1, RS3) are represented by purple bars.

them. He naturally became dominant male without having to dominate over a pride or defend a territory. Zulu may have also become accustomed to playbacks through prior studies conducted at the research site.

Similar to high appetitive playback scores, individuals with high territorial playback scores were more central to the groom network and more likely to initiate groom interactions as well as to self-groom. They were also more social and more likely to exhibit individual play behaviors. The correlation could reflect the fact that the offspring had generally higher territorial playback scores than adults and are naturally more playful as juveniles. I also observed that lions with high territorial playback scores were more likely to receive aggressive social interactions from other individuals. This correlation may be attributed to the fact that RS3, an offspring lioness with a higher than average overall boldness score, was the subject of numerous aggressive encounters during observations throughout this study. The statistical significance of these correlations may be seen in Appendix B.

In lion prides, it is well-known that lionesses hunt more than males (Schaller, 1972; Packer, Scheel, & Pusey, 1990). Previous studies also have shown that there is a possible sex bias for grooming, with females more likely to initiate and participate in grooming interactions (Schaller, 1972; Dunston et al., 2017). The results of my study support these observations, indicating that the Dambwa pride is behaving similarly to a wild pride. This provides encouraging evidence that the offspring studied are suited for release into the wild.

What Does This Mean for the Future of the Lion?

Understanding animal behavior is an important part of conservation management because it can help identify ineffective or inappropriate behavior that could cause management programs to fail (Berger-Tal & Saltz, 2016). The concern is that if the conditions captive lions were raised in did not adequately prepare them for the wild, they may have altered temperaments with maladaptive behaviors, which

could lead to changes in their responses to human contact and their hunting abilities and affect reproductive success (McDougall, Réale, Sol, & Reader, 2006; Berger-Tal & Saltz, 2016). Therefore, it is especially important to identify these potential maladaptive behaviors before reintroduction to ensure the success of captive-raised individuals. It is important to note that the results of my study indicate that, compared to previous research, the Dambwa pride is exhibiting natural behaviors similar to that of a wild pride.

The success of ex-situ reintroduction programs like the one being implemented at ALERT has been largely disputed (Dunston et al., 2017). Therefore, extensive measures and assessments must be taken to ensure that individuals chosen for release exhibit appropriate behaviors best suited for survival (Berger-Tal & Saltz, 2016; Dunston et al., 2017). The sub-adult lions that were part of my research study will not be released for at least another one to two more years. Long-term monitoring and assessment of behavior and boldness will need to continue on the six offspring prior to and after their release into the wild.

My study provides insight into lion personality, which is a critical component to determining the composition of a functional lion pride. My study also provides insight into individual personality traits, such as boldness, which need to be identified prior to release in order to determine correlation with survival after release.

Continued observation will show whether boldness scores correlate with survivorship and success after reintroduction. With further research coupled with careful monitoring of postrelease success of ex-situ individuals, boldness tests of the African lion have the potential to become a critical tool to support prerelease assessments and program success.

Concluding Thoughts

During my nine weeks in Africa, I learned so much more than I anticipated from the people at ALERT, the local people of Livingstone, Zambia, and, most importantly, the lion pride I studied. This research trip was my first time traveling alone outside of the United States. It helped me become more independent, exposed me to a variety of cultures from around the world, and cultivated a new love of traveling. Through this project, I have become incredibly passionate about African lion conservation. Programs such as ALERT, coupled with research projects like mine, are crucial to the success of the species. I sincerely hope that the declining lion population can rebound and return to the thriving population it once was.

This trip has prepared me for my next step: veterinary school. I gained valuable field experience and got to work with an animal that I love. The memories I made, and the people I met along my journey, will stay with me for years to come.

I could not have completed this project without the help of my amazing foreign mentors, Emma Dunston and Jackie Abell, and my UNH mentor Drew Conroy. I want to thank Drew especially for pushing me to pursue this project since the first semester of my first year and for seeing the project through until the end with me. Special thanks to the African Lion and Environmental Research Trust (ALERT) for allowing me to conduct research at their beautiful Livingstone facility, and also to Emma

Dunston for helping me through data collection and analysis and always making me smile. I also want to thank all the people I met while conducting my research in Africa; I couldn't have done it without all of you. Lastly, I want to thank the Hamel Center for Undergraduate Research and my donors—Mr. Dana Hamel, the Frank R. and Patricia S. Noonan International Research Fund, and the Class of 1952 International Research Fund—for making this once-in-a-lifetime opportunity possible.

Category	Did not respond	YES	NO
Observed to hear playback?	0	1	0
Observed to stand in response? (if previously sitting or lying down)	0	1	0
Roared in response	0	1	0
Snarl or have a defensive facial expression?	0	-1	0
Move 5 metres towards playback?	0	1	0
Move 5-10 metres towards playback?	0	1	0
Move 10-20 metres towards playback?	0	1	0
Move 20-50 metres towards playback?	0	1	0
Move >50 metres towards	0	1	0
Number of pauses during approach?	0	1-3 pauses = -1 4-6 pauses = -2 >7 pauses = -3	1
Retreats up to 5 metres from playback	0	-1	0
Retreats 5-10 metres from	0	-1	0
Retreats 10-20 metres from playback?	0	-1	0
Retreats 20-50 metres from playback?	0	-1	0
Retreats >50 metres from	0	-1	0
Number of pauses during retreat?	0	1-3 pauses = 1 4-6 pauses = 2 >7 pauses = 3	0
Retreats behind a physical barrier from playback?	0	-1	0
Seeks a higher position	0	1	0
Sniffs Air	0	1-3 sniffs = 1 4-6 sniffs = 2 >7 sniffs = 3	0
Time Spent Engaged	0	0-5 min = 1 5-10 min = 2 10-15 min = 3 15-20 min = 4 20-25 min = 5 25-30 min = 6 >30 min = 7	0
Follows another pride member?	0	-1	0

Appendix A

Scoring system adapted from Dunston et al. (2017) used to determine boldness scores for each playback. A score of +1 was associated with bold responses, such as approach or seeking an elevated position. A score of -1 was associated with fearful responses, such as retreat or following another pride member. Repetitive bold or fearful behavior resulted in multiple positive or negative scores.

Appendix B

Spearman's rank correlations were conducted to assess significance of correlations between sociality (as expressed in Figure 2), average percent daily activity (as expressed in Figure 3), and appetitive and territorial boldness (shown in Figures 4 and 5). The numbers were analyzed using values for all members of the pride. Significant correlations are highlighted in yellow.

APPETITIVE BOLDNESS TEST		
BEHAVIOR/SOCIAL MATRIX	CORRELATION	P-VALUE
ABNORMAL	-0.131	0.167
AGGRESSION BETWEENNESS	0.307	0.08
AGGRESSION INDEGREE	0.371	0.057
AGGRESSION OUTDEGREE	-0.105	0.183
ALL SOCIAL BETWEENNESS	0.187	0.139
ALL SOCIAL INDEGREE	0.245	0.108
ALL SOCIAL OUTDEGREE	0.592	0.011
DEFECATION	0.332	0.072
FEEDING	-0.358	0.062
GREET BETWEENNESS	0.291	0.089
GREET INDEGREE	0.175	0.143
GREET OUTDEGREE	0.589	0.011
GROOMING	0.377	0.055
GROOM BETWEENNESS	0.594	0.011
GROOM INDEGREE	0.031	0.23
GROOM OUTDEGREE	0.72	0.002
LOCOMOTION	0.152	0.159
PLAY	0.297	0.086
PLAY BETWEENNESS	-0.119	0.175
PLAY INDEGREE	-0.059	0.213
PLAY OUTDEGREE	0.138	0.167
RESTING	0.056	0.213
SOCIAL	0.585	0.012
UNKNOWN	-0.52	0.021
VISUAL	-0.354	0.064

TERRITORIAL BOLDNESS TEST		
BEHAVIOR/SOCIAL MATRIX	CORRELATION	P-VALUE
ABNORMAL	0.088	0.196
AGGRESSION BETWEENNESS	0	0.248
AGGRESSION INDEGREE	0.424	0.042
AGGRESSION OUTDEGREE	-0.346	0.067
ALL SOCIAL BETWEENNESS	-0.196	0.132
ALL SOCIAL INDEGREE	-0.108	0.183
ALL SOCIAL OUTDEGREE	0.327	0.072
DEFECATION	0.286	0.089
FEEDING	-0.488	0.026
GREET BETWEENNESS	-0.208	0.23
GREET INDEGREE	-0.383	0.052
GREET OUTDEGREE	0.186	0.139
GROOMING	0.622	0.008
GROOM BETWEENNESS	0.516	0.021
GROOM INDEGREE	0.195	0.132
GROOM OUTDEGREE	0.469	0.03
LOCOMOTION	0.334	0.069
PLAY	0.446	0.035
PLAY BETWEENNESS	-0.202	0.128
PLAY INDEGREE	-0.252	0.104
PLAY OUTDEGREE	0.342	0.067
RESTING	-0.063	0.209
SOCIAL	0.67	0.005
UNKNOWN	-0.545	0.017
VISUAL	-0.053	0.217

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Author and Mentor Bios

Courtney Kamyk had an amazing time working with both people and animals during her International Research Opportunities Program (IROP) experience during the summer of 2017. She was excited to put her lifetime passion for animals, especially her soft spot for big cats and African wildlife, to use in studying animal behavior. With her *Inquiry* article, she hopes to spread a message of conservation awareness to a wide audience. Courtney came to the University of New Hampshire (UNH) from Rutland, Vermont to major in animal science and minor in animal behavior, and completed her honors thesis on her research in Africa. After graduating from UNH in May 2018 with a bachelor of science degree, Courtney will attend Tuft's Cummings School of Veterinary Medicine, where she intends to apply what she learned from her valuable experience in Zambia.

Andrew Conroy, a professor of applied animal science and integrated agriculture within the Thompson School of Applied Science, has taught at the University of New Hampshire (UNH) since 1990. Dr. Conroy's specialty is cattle, but he has global experience with other livestock, animal handling, and applied animal behavior. He has conducted research in Africa, including research with pastoral people in Tanzania and Namibia. Dr. Conroy spent 2008 in Namibia and 2016 in Rwanda as a Fulbright Scholar. While abroad, he investigates organizations where UNH students could do internships or supervised research in wildlife management and wildlife conflict. He has worked with twelve UNH undergraduates conducting research abroad, including projects with cheetahs, elephants, and black rhinos in Africa and with koalas in Australia. After seeing one of Dr. Conroy's lectures about his work in Africa, Courtney Kamyk knew she had found someone who could help her follow her childhood dream of working in Africa with lions. Dr. Conroy said, "Courtney pushed me to find her a place to work in Zambia [a new country for him] and, with studying lion behavior, explore a new species struggling to survive in Africa."

Jackie Abell is the director of research for the African Lion and Environmental Research Trust (ALERT) in Zimbabwe and in Zambia. Dr. Abell is also a reader in psychology at Coventry University in the United Kingdom. Her research and teaching focus is on ex-situ reintroduction, lion conservation, social and conservation psychology, and qualitative and quantitative methods, including social network analysis. Dr. Abell has mentored undergraduate researchers many times over the past twenty years, and she supervised Dr. Emma Dunston as Courtney's co-mentor in Zambia.

Emma Dunston is a current casual lecturer and casual research technician in animal behavior and welfare at Charles Sturt University in Australia. She is especially interested in studying social behavior and individual personality in animals. In any work she undertakes, Dr. Dunston wishes to make an impact on the management and conservation of the species she works with. At the time of Courtney's research, Dr. Dunston was the principal researcher of the Dambwa Release Pride at the African Lion and Environmental Research Trust (ALERT), and supervised interns from around the world. Courtney's project was based on an article previously published by Dr. Dunston in the *Journal of Ethology*. As Courtney's mentor, she supervised data collection in the field and data analysis.